

Effects of scale on hunter moose *Alces alces* observation rate

Author: Sylvén, Susanne

Source: Wildlife Biology, 6(3) : 157-165

Published By: Nordic Board for Wildlife Research

URL: <https://doi.org/10.2981/wlb.2000.011>

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Effects of scale on hunter moose *Alces alces* observation rate

Susanne Sylvén

Sylvén, S. 2000: Effects of scale on hunter moose *Alces alces* observation rate. - Wildl. Biol. 6: 157-165.

Effects of sampling/observation area size on correlations between hunter moose *Alces alces* observation rates and moose density estimates have been evaluated. Each correlation between observation rates and moose density estimates was examined to discover extreme values strongly influencing correlations due to small sample sizes. The results of my study suggested that hunter observation rates were affected by sampling area size. Correlations between observation rates and moose densities indicate that there is a positive asymptotic relationship between hunter observation rate accuracy and sampling area, i.e. as the sampling area increases, so does the accuracy of the hunter observation rate. It was concluded that the accuracy of density estimates could be improved by using hunter observation rates obtained in sampling areas larger than 500 km². The concordance between moose counts and densities at this sampling area size was intermediate ($r_s = 0.5-0.7$). It is suggested that estimates of smaller management units may be improved when using year-to-year surveys at sampling within homogeneous management units. However, the confidence intervals are generally wide, and moose regulation authorities using hunter observation rates as a moose density estimator will have to accept estimates with a relatively low precision.

Key words: *Alces alces*, hunter, management, observation, sampling, survey

Susanne Sylvén*, Swedish Association for Hunting and Wildlife Management, Research Unit, Bäcklösavägen 8, SE-756 51 Uppsala, Sweden

*Present address: Department of Conservation Biology, Swedish University of Agricultural Sciences, Box 7002, SE - 750 07 Uppsala, Sweden - e-mail: Susanne.Sylvén@nvb.slu.se

Received 30 March 1999, accepted 13 July 2000

Associate Editor: Bernt-Erik Sæther

To effectively manage a game species its population dynamics must be thoroughly understood. Sæther (1997) and Solberg, Sæther, Strand & Loison (1999) illustrated how environmental stochasticity can affect populations of large herbivores. They also found that harvesting may have long-term effects on the population dynamics of ungulates. Lack of surveys and sporadic or biased surveys of such populations may result in local or regional populations getting totally out of control.

The moose *Alces alces* is no exception, and the high population growth potential of this species (Cederlund & Markgren 1987, Cederlund & Bergström 1996) underlines the need for a reliable survey method. Several methods have been proposed for use in detecting population trends (Caughley & Sinclair 1994). Aerial surveys are considered to be the most accurate method although dependent on a number of more or less well-controlled factors (Caughley 1974, Timmerman 1974, Gasaway & Dubois 1987, Stein-

horst & Samuel 1989). However, aerial surveys are costly. A much cheaper alternative is to utilise information provided by the thousands of hunters that observe moose each year, and calculate the number of moose observations per hunter day (MOHD), particularly early in the hunting season, in all kinds of habitats. This method has frequently been used in Fennoscandia during the last few decades (Jaren 1992, Nygren & Pesonen 1993, Ericsson & Wallin 1996). The observation rate (observations per time unit) is assumed to index population density (Ericsson & Wallin 1999, Solberg & Sæther 1999). Thus, in Sweden a large number of small areas are surveyed annually by hunting teams associated with these areas. Around 250,000 people hunt moose each year in Sweden (Ekman 1992), and during the first seven moose-hunting days in 1997 roughly 4.5 million hours were spent on moose hunting by Swedish hunters (J. Kindberg, Swedish Association for Hunting and Wildlife Management, Research Unit, Uppsala, pers. comm. 1998). In contrast to aerial surveys, MOHD estimations do not have to be made in mid-winter. As a consequence, MOHD data, which are collected in the hunting season, are not dependent on 'good' snow conditions as are aerial surveys. Another advantage is that no calculations of population changes from winter to the opening of the hunting season have to be made. Although MOHD estimates can be used to monitor changes in moose population density and annual reproduction (Fryxell, Mercer & Gellately 1988, Ericsson & Wallin 1999, Solberg & Sæther 1999), much of the basic knowledge regarding the relationship between moose observations and population density is still lacking (Crichton 1993, Ericsson & Wallin 1994).

My present study focused on determining how large a sampling area should be for it to provide useful MOHD estimates. Hunters tend to use small areas; one hunting team may cover 20–40 km² or less. County authorities consider local hunting club territories to be suitable as survey units for MOHD estimates (Thelander, Geibrink & Geibrink 1986). In central Sweden (excluding the island of Gotland) individual club territory units encompass areas of 77–4,650 km² (N = 119; J. Kindberg, Swedish Association for Hunting and Wildlife Management, Research Unit, Uppsala, pers. comm. 1998), whereas scientists refer to large areas, e.g. 1,700–2,800 km² (Fryxell et al. 1988, Solberg & Sæther 1999). Generally the precision of an estimate is expected to improve with the size of the count area. Furthermore, with larger sam-

pling areas, the likelihood of observing a moose increases (assuming that neither moose activity nor observation activity per km² show spatial variation) and the likelihood of only including partial home ranges in the survey decreases. Thus a large sampling area should contain a higher number of resident moose, compared with smaller areas (Wallin, Ericsson & Cederlund 1995). In a simulation study, Ericsson & Wallin (1994) found that to detect a 10% change in density a minimum effort of 5,500–8,500 observation hours was required. Assuming that a person spends on average 6.8 hours (G. Ericsson, pers. comm.) hunting per day, such a high number of observation hours can only be accumulated in large management units. Consequently, a sampling area should not be too small.

In this study, I analysed the effects of sampling/observation area sizes on the concordance between MOHD estimates and moose population density estimates. The objective was to determine the minimum size of a sampling area that can be used to obtain reliable population estimates by moose regulation authorities. I used MOHD data together with density estimates obtained from aerial surveys and official numbers of moose harvested. Furthermore, I controlled for regionally different relationships to sampling effort (hunter days: HD) and potentially biased correlations due to the occurrence of extreme values in the area size intervals due to few samples.

Material and methods

Study area

Data were collected in 10 years over a 17-year period in four counties, Södermanland (county D), Dalarna (county W), Gävleborg (county X) and Västernorrland (county Y), all situated in central Sweden (Table 1, Fig. 1). In total, I examined 27 management units distributed over coastal and inland habitats (see Fig. 1). Of the 27 management units, seven were surveyed for two or three years (mean: 2.43 times/unit). All other management units were surveyed once. The studied areas include farmland and productive forest habitats.

Hunter survey of moose

Moose observations and hunter days were recorded for each active hunting day during the first week of the moose hunt. Hunting teams were asked to record the number of hunters (observational effort), the

Table 1. Number of management units and years analysed, moose density estimates at the onset of hunt, and correction factors for aerial surveys for the four counties (see Fig. 1) surveyed.

County	Number of management units	Number of different years	Moose density after correction		Correction factor of aerial survey	
			Mean \pm sd	N	Mean \pm sd	N
D	1	3	2.96 \pm 0.29	3	1.28 \pm 0.05	3
Y	4	4	1.75 \pm 0.36	6	1.13 \pm 0.06	5
X	10	5	1.31 \pm 1.12	14	1.14 \pm 0.07	6
W	12	7	1.17 \pm 0.29	18	1.15 \pm 0.06	5
Total	27	-	-	41	-	19

number of moose bulls, females with one or two calves, females without calves, solitary calves and unclassified moose. The observation period included all activities associated with the hunt during the day. From these data, the observation rate (MOHD) was calculated as:

$$\text{MOHD} = \sum N_{\text{obs}} / \sum (N_{\text{hunters}} * N_{\text{days}}),$$

where N_{obs} is the number of moose observed, N_{hunters} is the number of hunters and N_{days} is the length of the observation period. Corrections were not made for double observations or moose shot. Owing to high levels of radioactive caesium in the moose meat following the Chernobyl nuclear accident the hunt in Västernorrland was terminated after only a few days or cancelled altogether in 1986. Therefore, MOHD data from county Y collected in 1986 were excluded from the calculations since they were not considered to be representative.

Estimates of moose population densities based on aerial surveys and harvest statistics

MOHD data were compared with the sum of the moose density data estimated from aerial surveys and official numbers of moose harvested. The aerial surveys were made during the winter, some months after the hunter survey, and the results were corrected (see Table 1) for sightability using standards established by Tärnhuvud (1988). Only density estimates from the most frequently used method (i.e. total area surveys by helicopters) were analysed in this study.

One uncertainty of the population estimate is that seasonal migration of moose may obstruct the interpretation of data collected especially from small sampling areas. Most of the sampling areas used in this study are situated in counties in south-central Sweden where long-distance moose migration does not occur (G. Cederlund, pers. comm.). Consequently movements in and out of a particular sampling area are assumed to remain approximately equal from the hunting period to the time of the aerial survey. Nevertheless, migration does occur in northern Sweden (Sandegren & Sweanor 1988). However, as management areas in northern Sweden are overall larger to account for any effect of migration, no bias towards either hunting or wintering areas should be expected (Ericsson & Wallin 1999).

Unfortunately, for the largest management units, the only data available concerned numbers of adults (no sex data) and calves which prohibited a comparison with MOHD of different moose categories. Local areas were the smallest area size group for which aerial survey data and official harvest statistics were collected. Therefore, the two smallest sampling area size groups of hunter observations, i.e. MOHD of 'team patches' (recorded by the hunting team when hunting on the 'patches' associated with the team) and MOHD from the slightly larger 'local areas', were both compared with aerial and harvest statistic data of the local areas. MOHD from the larger sampling units were compared with estimates of moose density for the re-

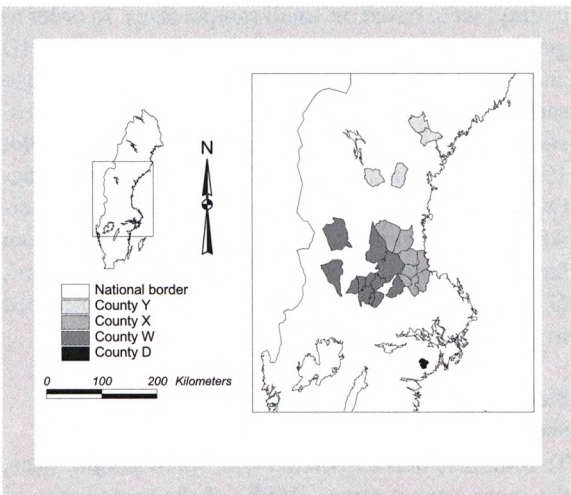


Figure 1. Location of the 27 management units included in the study which took place during 1978-1994 in the counties of Västernorrland (Y), Gävleborg (X), Dalarna (W) and Södermanland (D).

Table 2. Sample sizes, numbers of moose observed and hunter days used for survey, and area size (km²), given for each of the four sampling area sizes and according to county (see Fig. 1).

Sampling area size and county	Sample size N	Moose observed mean \pm sd	Hunter days mean \pm sd	Area size mean \pm sd
Team patches				
County X	13	22 \pm 10	35 \pm 15	23 \pm 20
County W	46	19 \pm 14	51 \pm 40	44 \pm 62
Local areas				
County D	12	89 \pm 58	104 \pm 60	37 \pm 22
County X	7	55 \pm 22	100 \pm 66	49 \pm 9
County W	18	49 \pm 29	131 \pm 77	49 \pm 10
Small management units				
County D	3	357 \pm 112	416 \pm 147	148 \pm 35
County Y	4	197 \pm 90	404 \pm 155	202 \pm 118
County X	9	341 \pm 216	608 \pm 489	243 \pm 132
County W	7	459 \pm 233	1145 \pm 628	308 \pm 68
Large management units				
County Y	2	642 \pm 323	1356 \pm 469	725 \pm 389
County X	4	1056 \pm 249	2633 \pm 829	699 \pm 222
County W	11	1349 \pm 677	3673 \pm 1831	1493 \pm 803

spective area size group, i.e. small and large management units.

Sampling within area size groups and counties

Data were grouped on the basis of county and size of the sampled area (Table 2). The sampling area groups used were hunting team patches (mean information provided by hunting teams about the searched hunting area; 48 km² \pm 9 (SD), N = 59), local areas (sampled area groups <80 km²; mean hunting areas: 52 km² \pm 12 (SD), N = 37), small management areas (sampled area groups 80–449.9 km²; mean: 285 km² \pm 117 (SD), N = 23) and large management areas (sampled area groups \geq 450 km²; mean: 1,216 km² \pm 756 (SD), N = 17). Most data from the two largest sampling area groups (large and small management units) were provided as MOHD summaries by the hunting authorities. Observations of hunting team patches and corresponding local areas were derived during three years from three intensively investigated small management units, one each in the counties D (Södermanland), X (Gävleborg) and W (Dalarna). Data on these groups were, due to step-wise pooling in groups of increasing area sizes, not independent between area size groups. This limits the correlations to be calculated within each group.

MOHD estimates were affected by county at the smallest sampling groups (hunting team patches: $F = 11.66$, $P = 0.0012$; local areas: $F = 20.51$, $P = 0.0001$; small management units: $F = 5.85$, $P = 0.0052$), but not at the large management unit group ($F = 1.07$, $P = 0.3691$). The data were divided into 10 groups according to sampling area size and differences found to be due to county (see Table 2). Correlations be-

tween MOHD and moose densities were calculated for each of the 10 groups.

Statistical models

The Statistical Analysis System (SAS Institute Inc. 1989) was used. Analyses of variance were employed to detect differences of MOHD between counties, regressions of MOHD on HD nested within county and estimated moose densities nested within county were used to examine for sampling effect, and correlations were used to evaluate the relationship between MOHD and moose density estimates. Owing to skewed data, the team patch data were log₁₀ transformed. Spearman correlations (r_s) were used because most of the groups (unique for area size and county) were based on small sample sizes. In order to get an overview of the correlations between MOHD and moose density estimate in relation to the average sampling area sizes of the groups a non-linear regression was fitted to all correlation estimates (SigmaPlot 1997). In addition, an estimate of the correlation between MOHD and densities for the county of Västerbotten in northern Sweden (N = 31 samples from large management units, i.e. mean area of 2,197 km²; G. Ericsson & K. Wallin, pers. comm.) was included in this regression.

Reliability of data sets based on small sample sizes

To minimise bias associated with small sample sizes, the mean square errors (MSE) of the regressions of MOHD on density were examined using a Wilcoxon matched pairs signed-ranks test (Siegel & Castellan 1988). A data set involving 200 random observations

with the same mean and variance as the observed real data was simulated. From this simulated data set, 10 random data sets with a sample size equal to the real data set were randomly selected. To determine whether the MSE differed between the real data (observed) and the simulated random data (the 10 random data sets), a non-parametric Wilcoxon matched pairs signed-ranks test (one tailed, $P \leq 0.05$) was performed. A sample MSE which was lower for observed data than for random data was interpreted as an indication that the correlation coefficient is unlikely to be affected by sample size (or random extreme values); thus it would differ towards a lower MSE from correlations based on random data.

Results

Relationships between MOHD and sampling effort (HD)

In order to analyse MOHD for linear relationships with moose density estimates (MO) and/or sampling efforts (hunter days: HD), parts of the data were examined. Observations in this data set appeared only once and no pooling was performed. A multiple regression analysis of the relationship between the dependent variable MOHD and moose density estimates nested within county and sampling effort (HD) nested within county was significant ($N = 77$, $r^2 = 0.60$, $F = 12.77$, $P < 0.0001$). However, only the par-

tial effect between MOHD and moose density was significant ($F = 10.68$, $P < 0.0001$), and no partial significance was found between MOHD and HD ($F = 1.73$, $P = 0.1526$). Obviously the MOHD ratios within the counties showed linear relationship to the numerator moose densities, whereas there was no significant linear relationship between MOHD ratios and the denominator HD.

Effects of sampling area size on correlations between MOHD and moose densities

Although the correlations (r_s) generally increased with area size, large differences between counties were found (Fig. 2, Table 3). A positive asymptotic relationship was found between r_s and sampling area size (Fig. 3). Precision was generally low, and for the group of large management units less than half of the variation in MOHD was explained by moose density estimates (see Table 3; $r_{\text{pearson}} = 0.58$, $r^2 = 0.34$).

Reliability of the correlation estimates

Since correlation estimates may be seriously biased by small sample sizes, i.e. by extreme values, the reliability of the correlation estimates was examined by comparing simulated and statistically estimated values (Mean Square Error). This analysis revealed that the correlations based on observed data sets differed from those based on random data sets. The MSE was generally lower for observed data than for the random data (Wilcoxon matched pairs signed-ranks test,

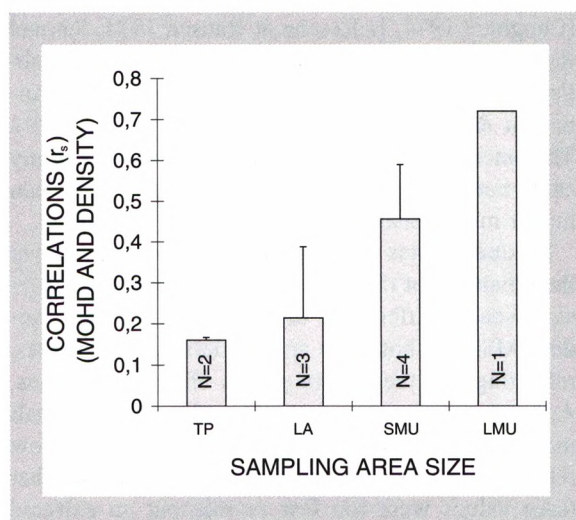


Figure 2. Spearman rank correlations (r_s ; mean \pm SE) between MOHD estimates and moose density estimates at the four sampling area size groups, TP (team patches), LA (local areas), SMU (small management units) and LMU (large management units). Number of analysed counties at each sampling area size group is indicated inside the bars.

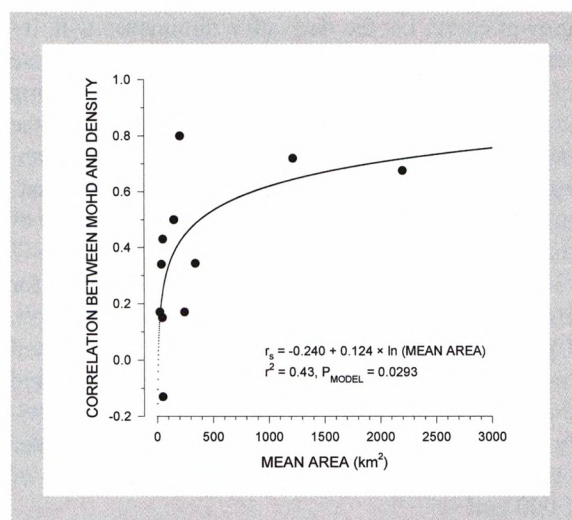


Figure 3. Asymptotic relationship found between the mean area size of the analysed county/area size groups and the Spearman rank correlation (r_s) between MOHD estimates and standard moose density estimates. The correlation estimate for the largest areas is based on data from the county of Västernorrland in northern Sweden (see Ericsson & Wallin 1999).

Table 3. Correlation (r_s) between MOHD estimates and standard moose density estimates, given for each of the four sampling area sizes and according to county (see Fig. 1). The results of Wilcoxon matched pairs signed-ranks test of the relation between MSE from correlations based on observed data sets and MSE from correlations based on random data sets indicate that correlations based on observed data sets differ from correlations based on random data sets.

Sampling area size/county	Sample size	Correlation	Wilcoxon signed-ranks	
		MOHD/moose density r_s	Observed MSE against random MSE T	P
Team patches				
County X	13	0.17	14	> 0.5
County W	46	0.15	1	> 0.5
Local areas				
County D	12	0.34	52	0.005
County X	7	0.43	51	0.007
County W	18	-0.13	31	0.385
Small management units				
County D	3	0.50	22	> 0.5
County X	9	0.17	40	0.116
County W	7	0.36	37	0.188
County Y	4	0.80	39	0.027
Large management units				
Counties X, W and Y	17	0.72	55	0.001

one tailed, $P \leq 0.05$) for both local and management unit sample sizes (see Table 3). In the Wilcoxon signed-ranks test, ties occurred among small management units in county Y (Västernorrland), thus nine pairs could be compared (instead of 10).

Discussion

The present results indicate that the correlation between MOHD estimates and moose density estimates improves as the size of the sampling area increases. The relationship is best described by an asymptotic growth curve, i.e. the derivative diminishes with increasing area. Thus, the use of MOHD as an estimate of moose density should be restricted to sampling areas larger than 500 km² in size. In Sweden, the hunting authorities have proposed that regional management units be used as sampling areas for estimating MOHD (Thelander et al. 1986). The mean size of management units in central Sweden ($655 \text{ km}^2 \pm 647$ (SD), $N = 119$; J. Kindberg, Swedish Association for Hunting and Wildlife Management, Research Unit, Uppsala, pers. comm. 1998) exceeds the suggested minimum size of 500 km². Kale (1982) suggested that in northern Canada moose could be satisfactorily managed based on estimates obtained from hunter observations in management units of a mean size of 1,000 km².

The accuracy of MOHD density estimates will rapidly increase with sampling area size up to ca 500 km². Above this level it should be kept in mind that the positive effects of increasing sampling area size

rapidly diminish as the asymptote is approached. A conflict between a potential improved precision and management use for units above 500 km² will call for a trade-off analysis. Are estimates based on MOHD in areas of this size accurate enough to detect changes in populations from one year to the next? To answer this question, four aspects of the estimate will be stressed.

First, the reliability of the estimated correlations may be questioned: MOHD estimates are correlated to density, which in my study was measured as the sum of shot moose and aerially surveyed moose. As the accuracy of aerial surveys may vary considerably (Caughley 1974, LeResche & Rausch 1974, Samuel & Pollock 1981), correction factors have to be established for each particular survey (Seber 1982, Anderson & Lindzey 1996, Ericsson & Wallin 1999). The 'uncertain' accuracy of the aerial surveys in my study may distort the estimated correlations between hunter moose counts and moose density estimates.

Second, effects of small sample sizes may lower the reliability of the correlation estimates. My analysis revealed differences between observed and random MSE for both low and moderate sample sizes, reflecting that there were effects of extreme values. At least one extreme value appeared among the small management units of county D. The comparably low reliability of this correlation ($P > 0.05$) indicates that three values were too few to rule out an extreme value effect, which the observations of 12 local areas before they were pooled to the three 'small' management areas did ($P = 0.005$). In conclusion, the result obtained comparing simulated and statistically esti-

mated values (MSE) can be seen as an indication that the correlation estimates reflect a real tendency.

Third, the number of hunter days (HD) is included in the variable MOHD. One can speculate whether the number of HD is similar in different regions and in areas of different sizes, but this type of information (hunter age, motives for hunting, experience, traditions, hunting regulations) is not available for this large data set and nor is it, so far, available in practise.

Fourth, the effect of sampling area on estimate precision caused by variance in the observed number of moose and the spatial variability of animals should be taken into account (Steinhorst & Samuel 1989). Knowledge of individual home range sizes in a population is also important. As the size of the sampling area increases, the proportion of whole home ranges within the sampling area will increase, thus resulting in more reliable moose observations. The largest home ranges have been found in northern Sweden (Wallin et al. 1995). This suggests that the optimal sampling area is larger in northern than in southern Sweden. Therefore, the conclusions of my study should not be skewed by a limited amount of small management units in northern Sweden.

In my study, the correlations between MOHD estimates and moose density estimates were highest in large management units (average $1,216 \text{ km}^2 \pm 756 \text{ (SD)}$). This conforms with the significant correlation found between MOHD and moose density estimates reported by Fryxell et al. (1988). These data were obtained in sampling areas $2,000\text{--}2,800 \text{ km}^2$ in size. My analysis showed that less than half of the variation in MOHD of the area size group 'large management units' was explained by estimated moose densities ($r^2 = 0.34$). The confidence intervals of these 'good' sampling area groups are generally wide, and moose regulation authorities using MOHD estimates have to accept a relatively low precision.

Management implications

Although large sampling areas should be used if MOHD estimates are to be accurate, most local moose management thus far has been based on relatively small units. The results of my analysis show that data from sampling units smaller than 500 km^2 in size should not be used if not adjusting for inherent variability of these data.

The minimum observation effort required to achieve a sufficient level of accuracy for a given management unit has to be identified. The variation in MOHD is

stochastic in nature because the sources of variation are more or less impossible to control. Demographic factors, the sightability/behaviour of moose categories, vegetation cover and observational effort (time used, ways of observing/hunting method) are among the factors affecting the reliability of MOHD estimates (Mercer & Manuel 1974, Crête, Taylor & Jordan 1981, Ferguson, Oosenburg & Mercer 1988, Fryxell et al. 1988, Timmerman, Whitlaw & Rodger 1993, Ericsson & Wallin 1996, Gustafsson & Cederlund 1994). The length of the observation period also affects the observation data (Ericsson & Wallin 1994), and the length of the period has to be optimised because time associated factors, such as harvested moose numbers, hunting regulations and defoliation, may contribute to the observation variation and confuse the analysis.

The sampling variation can probably be reduced or standardised by carrying out year-to-year surveys within homogeneous management units, i.e. by standardising factors such as hunting activity, observation activity and vegetation cover (Ferguson et al. 1988, Fryxell et al. 1988, Anderson & Lindzey 1996) sampling variation may be reduced. The factors may covary with regional characteristics (e.g. geographic area, vegetation cover, moose demography). To discern population trends, historical series lasting at least 4–5 years are required (Harris 1986, Courtois & Crête 1993).

This suggests that management solutions, e.g. survey methods, ought to be developed for blocks of similar conditions. The degree to which estimates can be improved by identifying factors affecting the results would be greatest for the smaller sampling areas, for which the correlation estimates are most sensitive. One can speculate whether standardisation of observation factors can increase the accuracy of smaller and more local sampling areas. However, other cost effective hunter-organised inventories, e.g. pellet-group counts (K. Wallin, G. Ericsson, R. Bergström, G. Cederlund & O. Liberg, unpubl. data) may turn out to be appropriate for certain sampling area size groups and/or regions.

In general, when moving northward the productivity of the vegetation and the proportion of deciduous forest decrease whereas the corresponding proportion of coniferous forest increases (Nilsson 1990). Other northward trends, e.g. larger properties, more searched area per hunter and more loose dogs searching for moose during the hunting season have also been found (S. Sylvén, unpubl. data), suggest that

observation rates and consequently the sampling area sizes are affected by latitude. Ericsson & Wallin (1999) reported differences in observation rates between counties. They also concluded that moose observations reflect population size and reproductive rate reasonably well. However, calibration of the observation rate with independent measurements of the moose density was set as a prerequisite for the use of observation indices, also in 'local' moose management. I agree with these authors, however, that until an acceptable calibration is implemented the reliability of MOHD estimates conducted within small sampling areas is questionable, and their use is not to be recommended.

Acknowledgements - I gratefully acknowledge the moose hunters, the hunters' agencies of Swedish Association for Hunting and Wildlife Management and the employees of the forest companies Korsnäs Marma AB and Stora AB who provided data. G. Ericsson and K. Wallin contributed with an estimate on large sampling areas in northern Sweden and valuable support. Jonas Lemel kindly offered statistical advice, and thanks should be given to him and Jonas Kindberg for assistance in the production of computerised figures. I am also grateful to R. Bergström, G. Cederlund, G. Ericsson, O. Liberg and K. Wallin, for giving me access to an unpublished manuscript, and to G. Cederlund, P. Edenhamn, L. Hansson, F. Karlsson and E.J. Solberg for reviewing the manuscript at different stages. My study was financed by the Swedish University of Agricultural Sciences, the Swedish Environmental Protection Agency and the Swedish Association for Hunting and Wildlife Management.

References

- Anderson, C.R. Jr & Lindzey, F.G. 1996: Moose visibility model developed from helicopter surveys. - *Wildlife Society Bulletin* 24: 249-259.
- Caughley, G. 1974: Bias in aerial survey. - *Journal of Wildlife Management* 38: 921-933.
- Caughley, G. & Sinclair, A.R.E. 1994: *Wildlife ecology and management*. - Blackwell Scientific Publications, Oxford, 334 pp.
- Cederlund, G. & Bergström, R. 1996: Trends in the moose-forest system in Fennoscandia, with special reference to Sweden. - In: DeGraaf, R.M. & Miller, R.I. (Eds.); *Conservation of faunal diversity in forested landscapes*. Chapman & Hall, pp. 265-281.
- Cederlund, G. & Markgren, G. 1987: The development of the Swedish moose population, 1970-1983. - *Swedish Wildlife Research, Supplement 1*: 55-61.
- Courtois, R. & Crête, M. 1993: Predicting moose population parameters from hunting statistics. - *Alces* 29: 75-90.
- Crête, M., Taylor, R.J. & Jordan, P.A. 1981: Optimization of moose harvest in southwestern Quebec. - *Journal of Wildlife Management* 45: 398-611.
- Crichton, V. 1993: Hunter effort and observations - the potential for monitoring trends of moose populations - a review. - *Alces* 29: 181-185.
- Ekman, H. 1992: Social and economic roles of game and hunting. - In: Bergström, R., Hultdt, H. & Nilsson, U. (Eds.); *Swedish Game - Biology and Management*. Svenska Jägarförbundet, Stockholm, Sweden, pp. 64-71.
- Ericsson, G. & Wallin, K. 1994: Antal älgar som ses - bara en fråga om hur många som finns? - In: *Att observera älg - en fråga om täthet, rörelse och synbarhet*. Swedish University of Agricultural Sciences, Department of Animal Ecology, Mimeo, 31 pp. (In Swedish).
- Ericsson, G. & Wallin, K. 1996: The impact of hunting on moose movements. - *Alces* 32: 1-10.
- Ericsson, G. & Wallin, K. 1999: Hunter observations as an index of moose *Alces alces* population parameters. - *Wildlife Biology* 5: 177-185.
- Ferguson, S.H., Oosenburg, S.M. & Mercer, E.W. 1988: Use of hunter statistics to estimate moose abundance for moose management areas in Newfoundland. - Newfoundland and Labrador Wildlife Division Internal Reports, Mimeo, 30 pp.
- Fryxell, J.M., Mercer, W.E. & Gellately, R.B. 1988: Population dynamics of Newfoundland moose using cohort analysis. - *Journal of Wildlife Management* 52: 14-21.
- Gasaway, W.C. & Dubois, S.D. 1987: Estimating moose population parameters. - *Swedish Wildlife Research, Supplement 1*: 603-617.
- Gustafsson, L. & Cederlund, G. 1994: Observerbarhet och förflyttningar hos älgar i samband med jakt. - In: *Att observera älg - en fråga om täthet, rörelse och synbarhet*. Swedish University of Agricultural Sciences, Department of Animal Ecology, Mimeo, 19 pp. (In Swedish).
- Harris, R.B. 1986: Reliability of trend lines obtained from variable counts. - *Journal of Wildlife Management* 50: 165-171.
- Jaren, V. 1992: Monitoring Norwegian moose populations for management purposes. - *Alces supplement 1*: 105-111.
- Kale, W. 1982: Estimation for 'smaller' management units in the Yukon. - *Alces* 18: 116-141.
- LeResche, R.E. & Rausch, R.A. 1974: Accuracy and precision of aerial moose censuses. - *Journal of Wildlife Management* 38: 175-182.
- Mercer, W.E. & Manuel, F. 1974: Some aspects of moose management in Newfoundland. - *Naturaliste canadien* 101: 657-671.
- Nilsson, N-E. (Ed.) 1990: *Swedish National Atlas, Skogen*. - Bokförlaget Bra Böcker, Högåns, 144 pp. (In Swedish).
- Nygren, T. & Pesonen, M. 1993: The moose population (*Alces alces* L.) and methods of moose management in Finland, 1975-1989. - *Finnish Game Research* 48: 46-53.
- Samuel, M.D. & Pollock, K.H. 1981: Correction of visi-

- bility bias in aerial surveys where animals occur in groups. - *Journal of Wildlife Management* 45: 993-997.
- Sandegren, F. & Sweanor, P.Y. 1988: Migration distances of moose populations in relation to river drainage length. - *Alces* 24: 112-117.
- SAS Institute Inc. 1989: SAS/STAT® User's Guide, Version 6, Fourth Edition, Volumes 1 & 2. 1686 pp & index 53 pp.
- Seber, G.A.F. 1982: The estimation of animal abundance and related parameters. 2nd ed. MacMillan. New York, 654 pp.
- Siegel, S. & Castellan, N.J., Jr 1988: Nonparametric statistics for the behavioural sciences. 2nd ed. - McGraw-Hill Book Company, Inc., New York, 399 pp.
- SigmaPlot version 4.0, 1997, SPSS Science, SPSS Inc., USA.
- Solberg, E.J. & Sæther, B-E. 1999: Hunters observations of moose *Alces alces* as a management tool. - *Wildlife Biology* 5: 107-117.
- Solberg, E.J., Sæther, B-E., Strand, O. & Loison, A. 1999: Dynamics of a harvested moose population in a variable environment. - *Journal of Animal Ecology* 68: 186-204.
- Steinhorst, R.K. & Samuel, M.D. 1989: Sightability adjustment methods for aerial surveys of wildlife populations. - *Biometrics* 45: 415-425.
- Sæther, B-E. 1997: Environment stochasticity and population dynamics of large herbivores: a search for mechanisms. - *Trends in Ecology and Evolution* 12: 143-149.
- Thelander, B., Geibrink, O. & Geibrink, H. 1986: Höstens älgobs-inventering i siffror. - *Svensk Jakt* 124: 198-202. (In Swedish).
- Timmerman, H.R. 1974: Moose inventory methods: a review. - *Naturaliste canadien* 101: 615-629.
- Timmerman, H.R., Whitlaw, H.A. & Rodger, A.R. 1993: Testing the sensitivity of moose harvest data to changes in aerial population estimates in Ontario. - *Alces* 29: 47-53.
- Tärnhuvud, T. 1988: Utveckling av metoder för älginventering. Flyginventering - Slutrapport. - Swedish University of Agricultural Sciences, Department of Wildlife Ecology, 25 pp. (In Swedish).
- Wallin, K., Ericsson, G. & Cederlund, G. 1995. Egna älgar - och andras. - *Svensk Jakt* 133: 236-239. (In Swedish).